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Evaluating the specificity of ecosystem indicators to fishing in a changing environment: A model comparison study for the southern Benguela ecosystem

Kelly Ortega-Cisneros[a,*], Lynne Shannon[b], Kevern Cochrane[a], Elizabeth A. Fulton[c,d], Yunne-Jai Shin[b,e]

[a] Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown 6140, South Africa
[b] Marine Research Institute and Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa
[c] CSIRO Oceans and Atmosphere, Hobart, Tasmania 7001, Australia
[d] Centre for Marine Socioecology, University of Tasmania, Hobart, Tasmania 7001, Australia
[e] Institut de Recherche pour le Développement (IRD), UMR 248 MARBEC, IRD-IFREMER-CNRS-UM, Université de Montpellier, Place Eugène Bataillon, Montpellier, France

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ABSTRACT

Ecological indicators used to monitor fishing effects in the context of climate change and variability need to be informative to enable effective ecosystem-based fisheries management. We evaluated the specificity of the response of ecosystem indicators to different fishing and environmental pressure levels using Ecosim and Atlantis ecosystem models for the southern Benguela ecosystem. Three fishing strategies were modelled to represent a variety of ways of targeting fishing within an ecosystem: one focused on low trophic levels (i.e. forage species), another on higher trophic levels (i.e. predatory fish) and a third tested fishing pressure across the full range of potentially exploitable species. Two types of environmental change were simulated for each fishing mortality scenario – random environmental variability and directional climate change. The specificity of selected ecological indicators (mean trophic level of the community, proportion of predatory fish, biomass/landings, mean intrinsic vulnerability and marine trophic index) was evaluated for different combinations of fishing strategy, fishing mortality and both types of environmental change. While there were mostly large differences in indicator values computed from the Atlantis and Ecosim models, the specificity of the ecological indicators considered under changing climate generally corresponded between the two models. Certain indicators (i.e. mean trophic level of the community) were less specific in detecting effects of fishing in the southern Benguela for some of the three fishing strategies modelled (i.e. high trophic level fishing strategy) under climate change. This helped refine the most appropriate indicator set for our system, reflecting the focus of a particular fishing strategy, and improved confidence in the suitability of these indicators for monitoring fishing effects in the Southern Benguela.

1. Introduction

Ecosystem indicators are useful tools to provide insights on marine ecosystems, and have been used for assessment and management purposes to support an ecosystem approach to fisheries management (Garcia et al., 2003; Garcia and Cochrane, 2005). Some of their applications include evaluation of ecosystem effects of fishing (Shin et al., 2012, 2010b), ecosystem status (Gascuel et al., 2016) and impacts of climate change on fisheries and fishing dependent communities (Cheung et al., 2010; Colburn et al., 2016). The performance of candidate indicators must be assessed against screening criteria, of which sensitivity and specificity are essential properties (Rice and Rochet, 2005; Rochet and Trenkel, 2003). Sensitivity refers to the capacity of an indicator to detect change in an ecosystem, while specificity to fishing refers to the confidence with which a variation in an indicator can be attributed to changes in fishing pressure or altered management arrangements (Houle et al., 2012). For an indicator to be of use in achieving effective ecosystem based management, there must be a clear association between the changes observed in the indicator and the changes in a given stressor (e.g. fishing, pollution) and the indicator must be informative and attributable even in the presence of environmental variability or other anthropogenic stressors.

* Corresponding author.
E-mail address: k.ortegacisneros@ru.ac.za (K. Ortega-Cisneros).

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Climate change is a ubiquitous anthropogenic factor affecting marine ecosystems. Its effects are evident as changes in temperature, wind and circulation patterns, precipitation, and sea level rise (among others). All have potentially profound consequences for marine ecosystems and their services to societies (Barange et al., 2014; Hoegh-Guldberg et al., 2010; Pörtner et al., 2014). An increase in the frequency and intensity of extreme events (e.g. temperature, precipitation) has also been associated with climate change, and is likely to continue (Schlegel et al., 2017; Seneviratne et al., 2012; Ummenhofer and Meehl, 2017). In upwelling systems, characterized by high natural variability, the climate change-driven trend in environmental drivers is not clearly distinguishable from decadal variability, making predictions of the effects of climate change challenging (Lluch-Cota et al., 2014). Nevertheless, Henson et al. (2017) found that under a business as usual scenario, the climate-change trend in environmental drivers will be identifiable from the background of natural variability in more than 50% of the ocean in the next 15 years. Likely increases in climate variability associated with climate change will result in the need to find a suite of sensitive and specific indicators able to disentangle fishing effects from environmental variability. Simulation experiments can assist the selection of candidate indicators by providing a control environment to test different fishing and environmental variability scenarios within controlled conditions (Houle et al., 2012).

Environmental variability and fisheries exploitation are considered the main drivers of the southern Benguela system (Blamey et al., 2012; Kirkman et al., 2015; Shannon et al., 2004; Smith and Jarre, 2011). For the southern Benguela, ecosystem indicators have been used to evaluate, compare and communicate its ecological status, determine ecosystem trends and the influence of both fishing and environmental variability (Lockerbie et al., 2016; Shannon et al., 2014, 2010; Shin et al., 2010a,b). Moreover, the sensitivity of ecosystem indicators to fishing have been evaluated for the southern Benguela using different ecosystem models (Smith et al., 2015; Travers et al., 2006). However, no studies have evaluated in detail the specificity of ecosystem indicators for this system. Although Shin et al. (2018) undertook a comparative specificity analysis across ecosystems, including an assessment based on a single model of the Southern Benguela, the lack of comparison between different model outputs has been highlighted. The use of comparative approaches across different ecosystem models to estimate the sensitivity and specificity of ecosystem indicators should be valuable, since it can address the uncertainty in model structure and assumptions underlying different ecosystem models. Moreover, if model-derived indicators show a good agreement between ecosystem models, this increases the confidence in model predictions and can assist the selection of a robust set of indicators that can be reliably applied in the system. In this study, we evaluated the specificity of the response of ecosystem indicators to fishing in the context of environmental change. The indicators were systematically tested against different fishing and environmental pressure levels using the Ecopath with Ecosim (EwE) and Atlantis ecosystem models for the southern Benguela system.

2. Materials and methods

2.1. Ecosystem models

The Atlantis (Fulton et al., 2011) and the Ecopath with Ecosim (EwE, Christensen and Walters, 2004) modelling frameworks were used in this study. The southern Benguela system, our study area, extends from the Orange River mouth (29°S, South African – Namibian border) to the city of East London (28°E), to a maximum depth of 500 m offshore and has a total area of ~220 000 km^2 (Shannon et al., 2003). In the Atlantis model of the Benguela and Agulhas Currents (ABACuS v2), the southern Benguela is divided into 18 boxes, with one to four depth layers; the EwE model is not spatially explicit. In ABACuS v2, vertebrates are represented as age-structured groups consisting of 10 age classes, while invertebrates are modelled as biomass pools. In the EwE model, groups such as horse mackerel, shallow- and deep-water hake are modelled as juvenile and adults while other groups such as anchovy and sardine are not age-structured (Shannon et al., 2008). The initial biomass, distribution and diets used in both models represent the conditions in the southern Benguela system during 1990–1999. Further details on the Atlantis and EwE models for the southern Benguela can be found in Ortega-Cisneros et al. (2017) and Shannon et al. (2004, 2008) respectively.

Fisheries in ABACuS v2 were originally forced using catch time series from 1990 to 2013. For this study, fisheries were represented using fishing mortality rates instead of catch time series to more easily allow for the construction of the various scenarios and to facilitate comparison with the EwE model, which uses fishing mortalities to determine the modelled catches. Detailed information on the time series of observed and modelled catch and biomass from ABACuS v2 using fishing mortalities can be found in Appendix 1. Most target species were fished in both ecosystem models, with the exception of mesopelagic fish and chub mackerel (included in the other small pelagic fish group in ABACuS), the catches of which are modelled in the EwE model but not in ABACuS v2.

2.2. Ecosystem indicators

Five ecosystem indicators were assessed, based on the set of indicators recommended by IndiSeas (Coll et al., 2016; Shin et al., 2010b). Specifically, the indicators were: the total biomass over catch ratio, the marine trophic index (MTI), mean intrinsic vulnerability (IVI), mean trophic level (TL) of the community and proportion of predatory fish (Table 1). The Intrinsic Vulnerability Index ranges from 1 to 100, with higher values indicating higher vulnerability (Cheung et al., 2007). Indicators such as mean lifespan and mean length were not evaluated, since EwE is not an age or size-structured model. The ecosystem indicators were calculated using information on those species in the model that are surveyed or retained by fishing in the southern Benguela. For the trophic level calculations, a fixed TL was used for each species in both models. IVI was calculated using information on retained finfish groups only since no IVI scores are available for invertebrates. Similarly, MTI was calculated for all retained species, with the exception of sardine, which has a TL < 3.25. Cephalopods were the only invertebrate group included in our indicator calculations.

The performance of the indicators was evaluated under a range of scenarios, including combinations of fishing strategy (i.e. which part of the food web is targeted), fishing mortality (i.e. differing levels of fishing pressure) and two types of environmental change - random environmental variability and directional climate change.

Table 1
List of indicators used in this study. Indicators were calculated from model outputs. B = biomass (tons), Y = catch (tons), IVI = intrinsic vulnerability index and TL = trophic level.

Indicator	Calculation	Data requirements[1]	References
Biomass/Landings	B/Y	All retained species	Shin et al., 2010b
Marine Trophic Index	$\frac{\sum_S TL_S Y_S}{\sum_S Y_S} TL_S > 3.25$	All retained species	Pauly and Watson, 2005
Mean Intrinsic Vulnerability	$\frac{\sum_S IVI_S Y_S}{\sum_S Y_S}$	All retained species	Cheung et al., 2007
Proportion of predatory fish	$B_{predatoryfish}/B_{surveyed}$	All pelagic and demersal surveyed species	Shin et al., 2010b
Trophic level of the community	$\frac{\sum_S TL_S B_S}{\sum_S B_S}$	All pelagic and demersal surveyed species	Cury et al., 2005

[1] Definition of retained and surveyed species follows Shin et al. (2010b).

2.3. Fishing and environmental change

Indicators were systematically tested against different fishing and environmental pressure levels. Three fishing strategies were implemented to represent a variety of fishing contexts, one that focused on low trophic levels (i.e. forage species), another concentrating pressure on higher trophic levels (i.e. demersal and predatory fish, chondrichthyans and large pelagics) and a third that assigned fishing pressure across the full range of potentially exploitable species. Hereafter, we referred to them as "LTL", "HTL" and "ALL" strategies, respectively. These fishing strategies were selected following the modelling guidelines from the IndiSeas working group to estimate the performance of ecosystem indicators (Fu et al., 2018; Reed et al., 2016; Shin et al., 2018). To allow comparability between models, the F_{MSY} (fishing mortality that results in the maximum sustainable yield) was derived for every exploited species from each model by iterating the fishing mortality rates over a wide range and plotting catches to find the stationary point (maximum) in the yield curve. F_{MSY} was calculated at a precision of $10^{-2}\,year^{-1}$ for both models. Using F_{MSY} as reference points in each model, fishing pressure was varied in a comparable way, with scenarios run at $\lambda * F_{MSY}$ where λ (fishing mortality multiplier) = 0.25, 0.5, 0.75, 1, 1.25, 1.5. The species fished at $\lambda * F_{MSY}$ were determined by the fishing strategy (i.e. LTL, HTL or ALL) while the target species that sat outside of the focus of the fishing strategy were fished at their current (average 2010–2013 levels for Atlantis and for EwE, 1978) fishing mortality levels. For example, in the LTL strategy, the fishing mortality of forage species such as anchovy, redeye herring, sardine among others was $\lambda * F_{MSY}$, while the fishing mortality of other target species, which were not the focus of this strategy (e.g. hakes, snoek, chondrichthyans), was maintained at a constant fishing mortality representing their current fishing levels. In the ALL strategy, the fishing mortality of all exploitable species was modified by the fishing multipliers. The use of fishing multipliers and F_{MSY} provides a practical way to test the effect of varying fishing pressure in a standardized way across different types of models and ecosystem case studies (Shin et al., 2018). A burn-in time of 40 years was used for both the Atlantis and EwE simulations, after which simulations including fishing were run for another 40 years, the average of the last 10 years was used for the calculation of indicators.

Modelled phytoplankton biomass was used as a proxy in EwE to represent both types of environmental change – directional and random. For the directional change, a set of multipliers (γ = 0.85, 0.9, 0.95, 1, 1.05, 1.1) was used to force changes in the modelled EwE phytoplankton biomass. The chosen multipliers fell within the range of variation observed for several ecosystems in the last decade (Boyce et al., 2010).

For the random environmental change scenario, phytoplankton biomass in EwE was forced by a random multiplier with a mean = 1 and a range of standard deviations (σ = 0.1, 0.2 and 0.3). The set of standard deviations was derived from calculations of the mean and standard deviation of the annual average Chlorophyll-a extracted from the MODIS Aqua spectral data for seven ecosystems in the world from 2003 to 2011 as part of the IndiSeas project (mean of standard deviation = 0.21, range = 0.01 to 0.69), explaining the range of the standard deviations (0.1–0.3) used here (Shin et al., 2018). A lognormal distribution was used to represent the distribution of phytoplankton biomass since biomass distribution across body size in marine ecosystems is considered to be uniform on a logarithmic scale (Sheldon et al., 1972).

In Atlantis, phytoplankton biomass is an emergent property resulting from processes such as upwelling and nutrient cycling and so direct forcing of phytoplankton biomass and productivity (as done for EwE) was not appropriate. Instead nutrient inputs from upwelling were used to produce the expected levels of variability in phytoplankton biomass.

To evaluate the combined effect of fishing and both types of environmental change in the southern Benguela, we ran simulations using combinations of fishing strategy (LTL, HTL and ALL), fishing mortality (six multipliers) and either random or directional change for both ecosystem models (Fig. 1). To determine the effect of directional change, one simulation was run for each combination of fishing strategies, fishing mortality (F_{MSY} multiplier) and phytoplankton biomass multipliers. For the random change, 30 runs were conducted for the EwE model, while five replicates were run for the Atlantis model. The last ten years of the simulations were used to calculate the mean trophic level of the community, proportion of predatory fish, biomass/landings, mean intrinsic vulnerability and the marine trophic index.

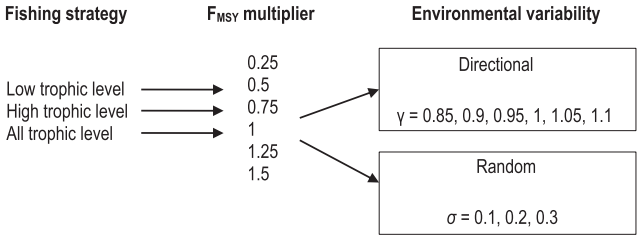

Fig. 1. Combinations of simulations accounting for fishing strategy, fishing mortality and type of environmental variability to determine the specificity of indicators to fishing. F_{MSY} = Annual fishing mortality rate at Maximum Sustainable Yield; σ = standard deviation of the lognormal distribution of phytoplankton biomass; γ = multiplier of phytoplankton biomass.

2.4. Specificity to fishing

The specificity of ecosystem indicators to the effects of fishing in the presence of directional environmental change was calculated by determining the ratio of the mean component of the fishing to phytoplankton biomass gradient following Shin et al. (2018). This allowed us to determine the degree of change in the response of indicators as a result of the systematic variation in fishing pressure and phytoplankton biomass levels. Indicators were standardized to the value of the indicator at a reference state defined by λ and γ multipliers being equal to 1. This reference value was subtracted from the value of an indicator at a particular combination of λ and γ multipliers and divided by the standard deviation of the indicator across multipliers for a given strategy. To determine the mean component of the fishing and phytoplankton gradients, the backwards difference between points for a given direction was calculated. For example, the gradient in the fishing component was calculated by determining the difference in the standardised indicators at λ = 1.5 and λ = 1.25, λ = 1.25 and λ = 1 and so on for each row (a particular γ). This resulted in two matrices, representing the components of the fishing and environmental (phytoplankton) gradients. The ratio of the mean fishing component of the gradient to the mean phytoplankton biomass component of the gradient was used to determine specificity to fishing. Values higher than 1 indicate that fishing has a stronger effect on the indicator response than changes in primary production, similarly, the higher the value the more specific the indicator is to fishing (Shin et al., 2018).

The signal-to- noise ratio was used to determine the specificity of indicators to fishing in the presence of random environmental variation. The signal is provided by the systematic change in fishing pressure levels and the noise by the simulated random change in phytoplankton biomass (Houle et al., 2012). First, the mean of the indicator values for each λ and σ was calculated from the replicates. The signal to noise ratio was calculated by subtracting the mean of an indicator at each λ with the mean of the indicator when λ = 1, and divided by the standard deviation of the indicator at the corresponding λ. The specificity was estimated by the absolute value of the slope of the linear regression between the signal-to-noise ratio and the fishing mortality multipliers. A higher absolute value of the slope indicates higher specificity of an indicator to fishing (Houle et al., 2012).

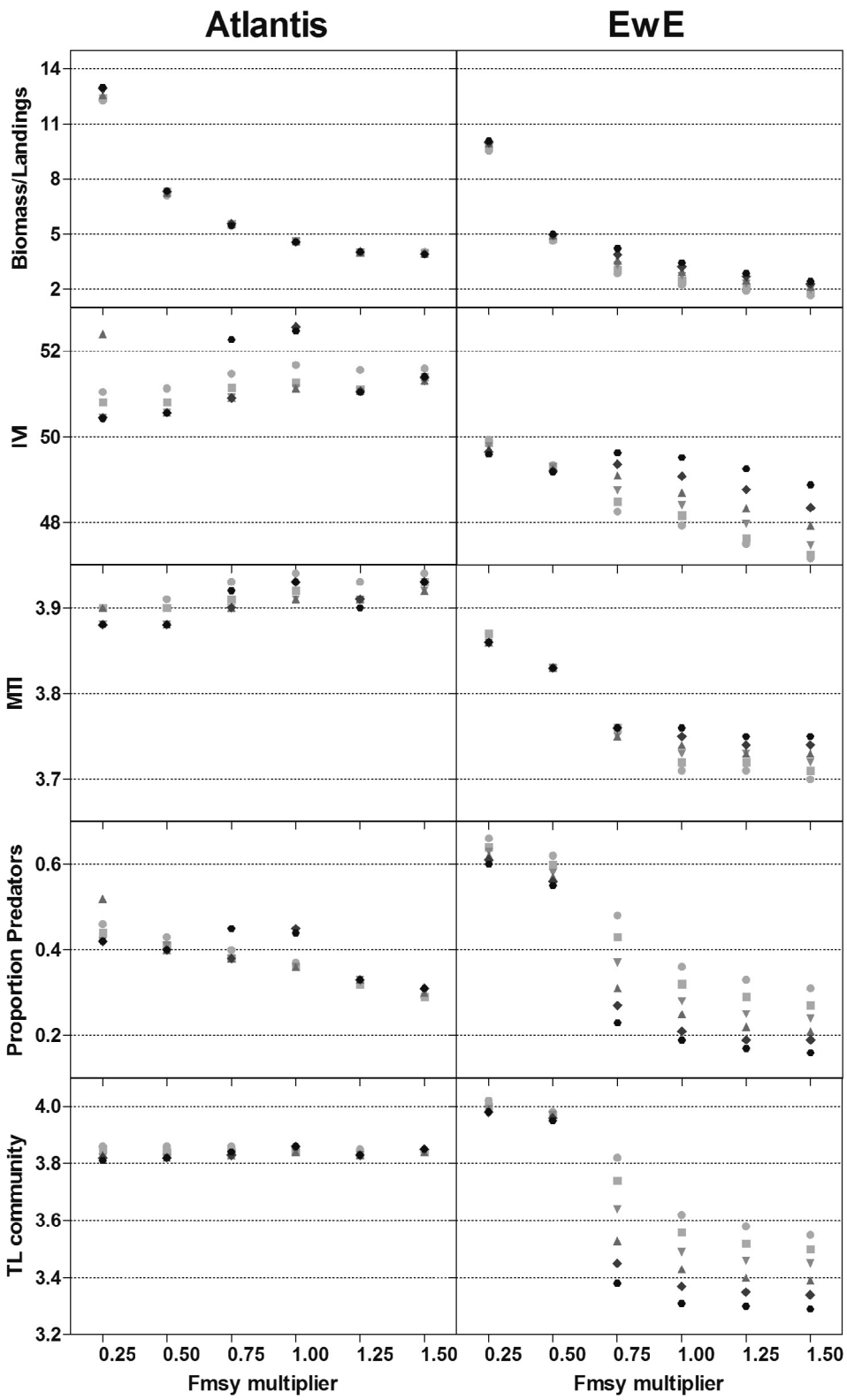

Fig. 2. Indicators derived from the Atlantis and EwE models of the southern Benguela system for the ALL fishing strategy across F_{MSY} and phytoplankton biomass multipliers under directional change. Symbols represent phytoplankton multipliers, 0.85 = circle, 0.9 = square, 0.95 = inverted triangle, 1 = triangle, 1.05 = rhombus and 1.1 = hexagon. IVI = Intrinsic vulnerability Index, MTI = Marine Trophic Index, TL community = Trophic level of the community.

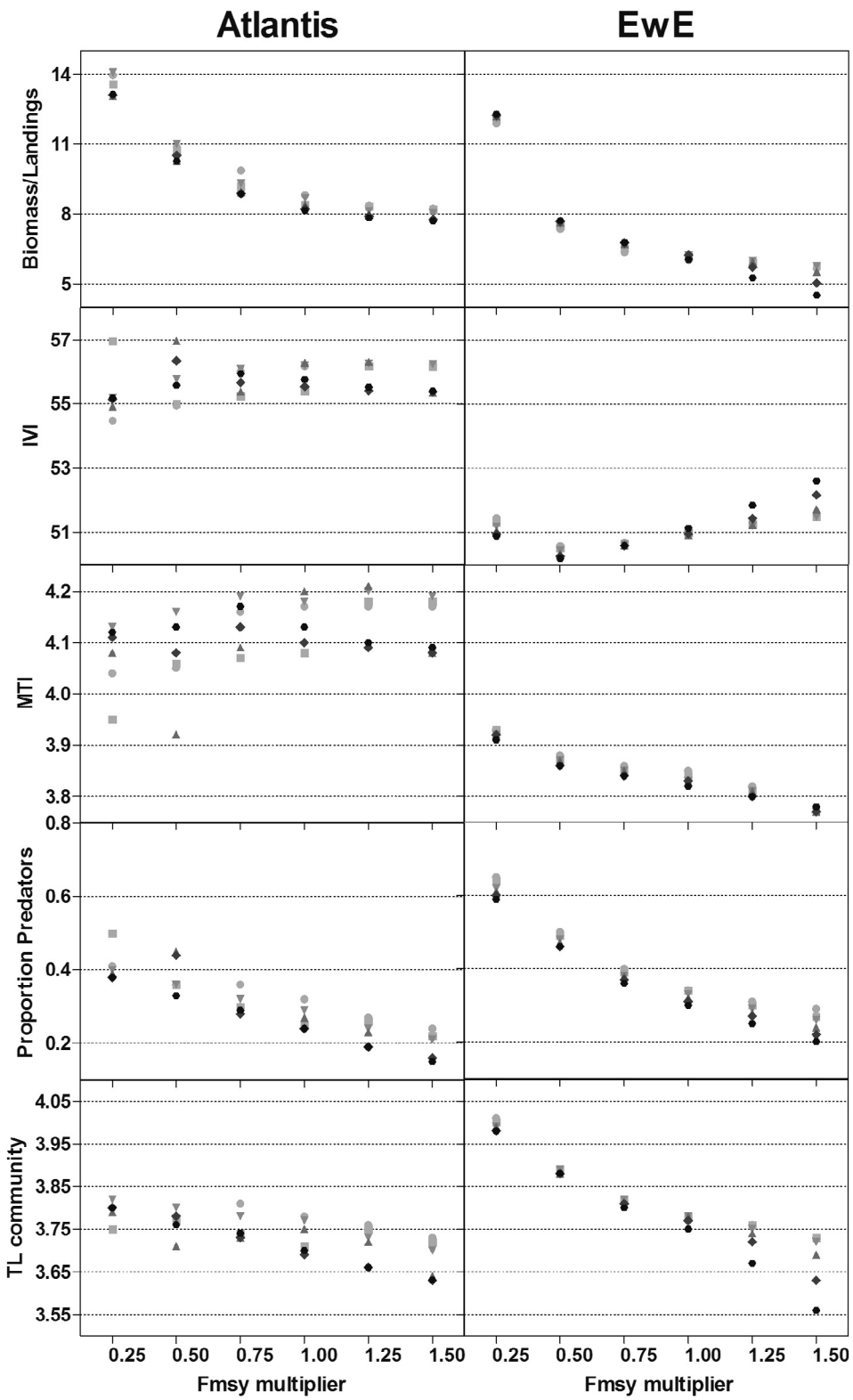

Fig. 3. Indicators derived from the Atlantis and EwE models of the southern Benguela system for the HTL fishing strategy across F_{MSY} and phytoplankton biomass multipliers under directional change. Symbols represent phytoplankton multipliers, 0.85 = circle, 0.9 = square, 0.95 = inverted triangle, 1 = triangle, 1.05 = rhombus and 1.1 = hexagon. IVI = Intrinsic vulnerability Index, MTI = Marine Trophic Index, TL community = Trophic level of the community.

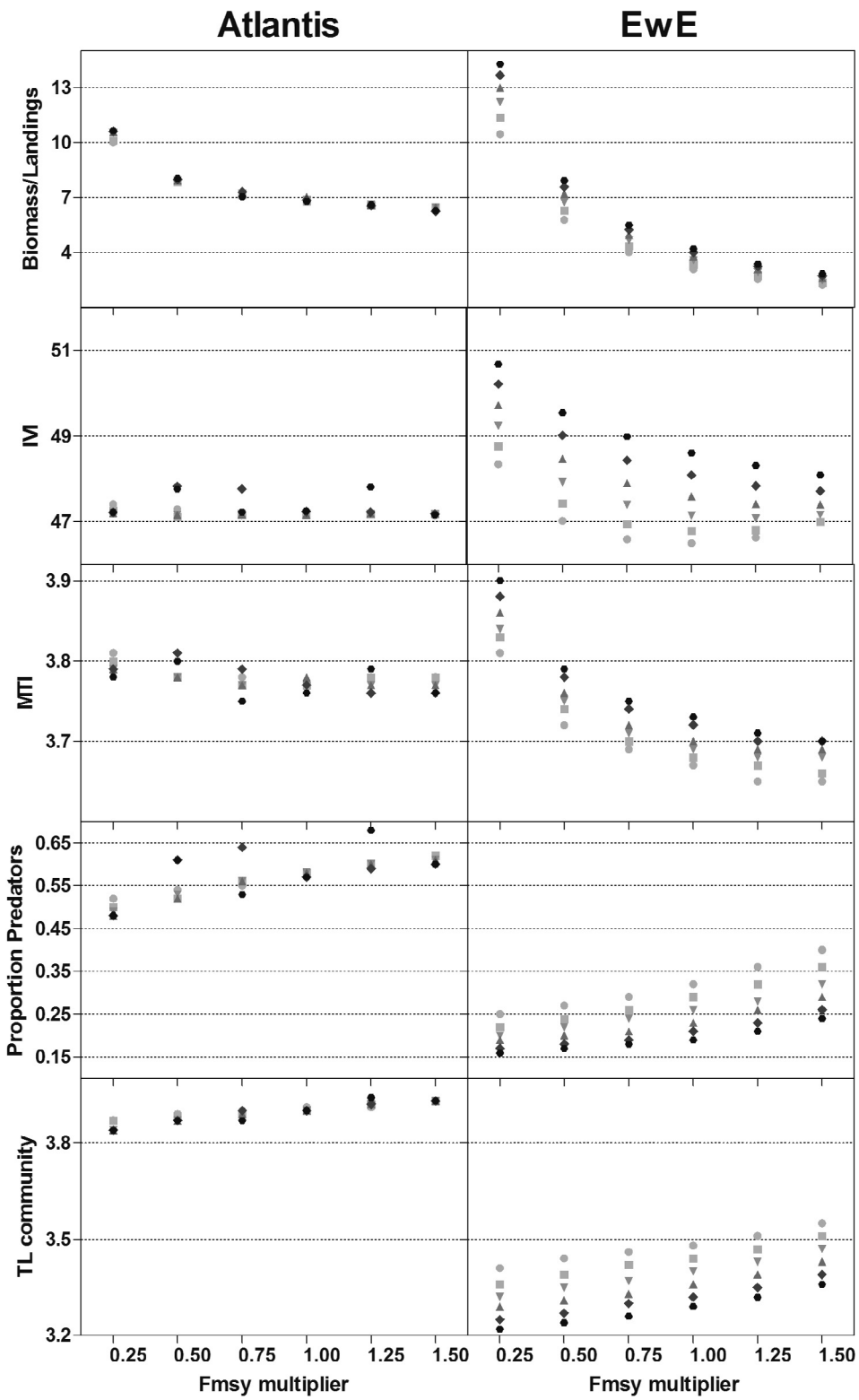

Fig. 4. Indicators derived from the Atlantis and EwE models of the southern Benguela system for the LTL fishing strategy across F_{MSY} and phytoplankton biomass multipliers under directional change. Symbols represent phytoplankton multipliers, 0.85 = circle, 0.9 = square, 0.95 = inverted triangle, 1 = triangle, 1.05 = rhombus and 1.1 = hexagon. IVI = Intrinsic vulnerability Index, MTI = Marine Trophic Index, TL community = Trophic level of the community.

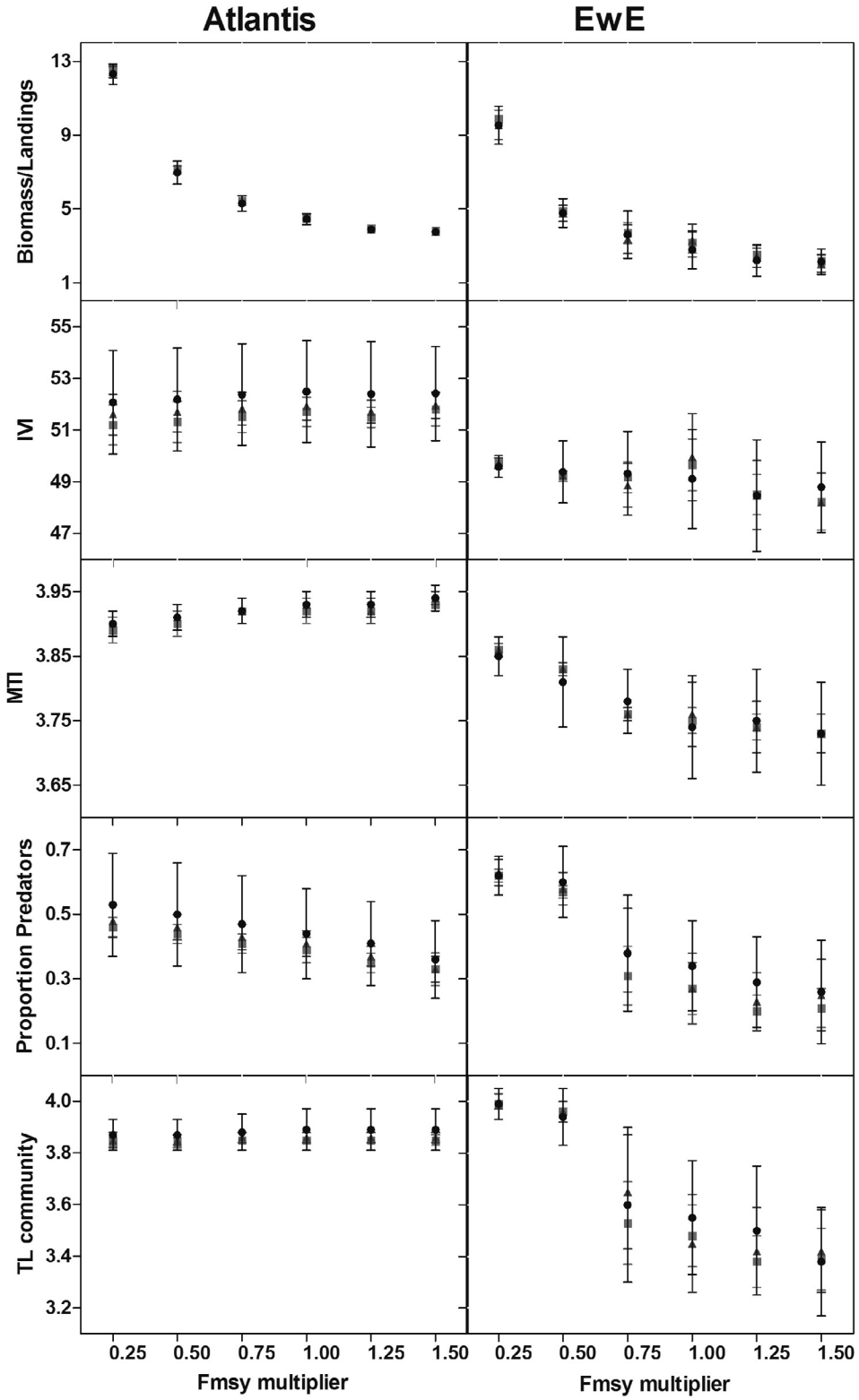

Fig. 5. Indicators (Mean ± SD) derived from the Atlantis and EwE models of the southern Benguela system for the ALL fishing strategy across F_{MSY} and random multipliers of phytoplankton biomass. Symbols represent the standard deviation values of the multipliers for the phytoplankton biomass, 0.1 = square, 0.2 = triangle and 0.3 = circle. IVI = Intrinsic vulnerability Index, MTI = Marine Trophic Index, TL community = Trophic level of the community.

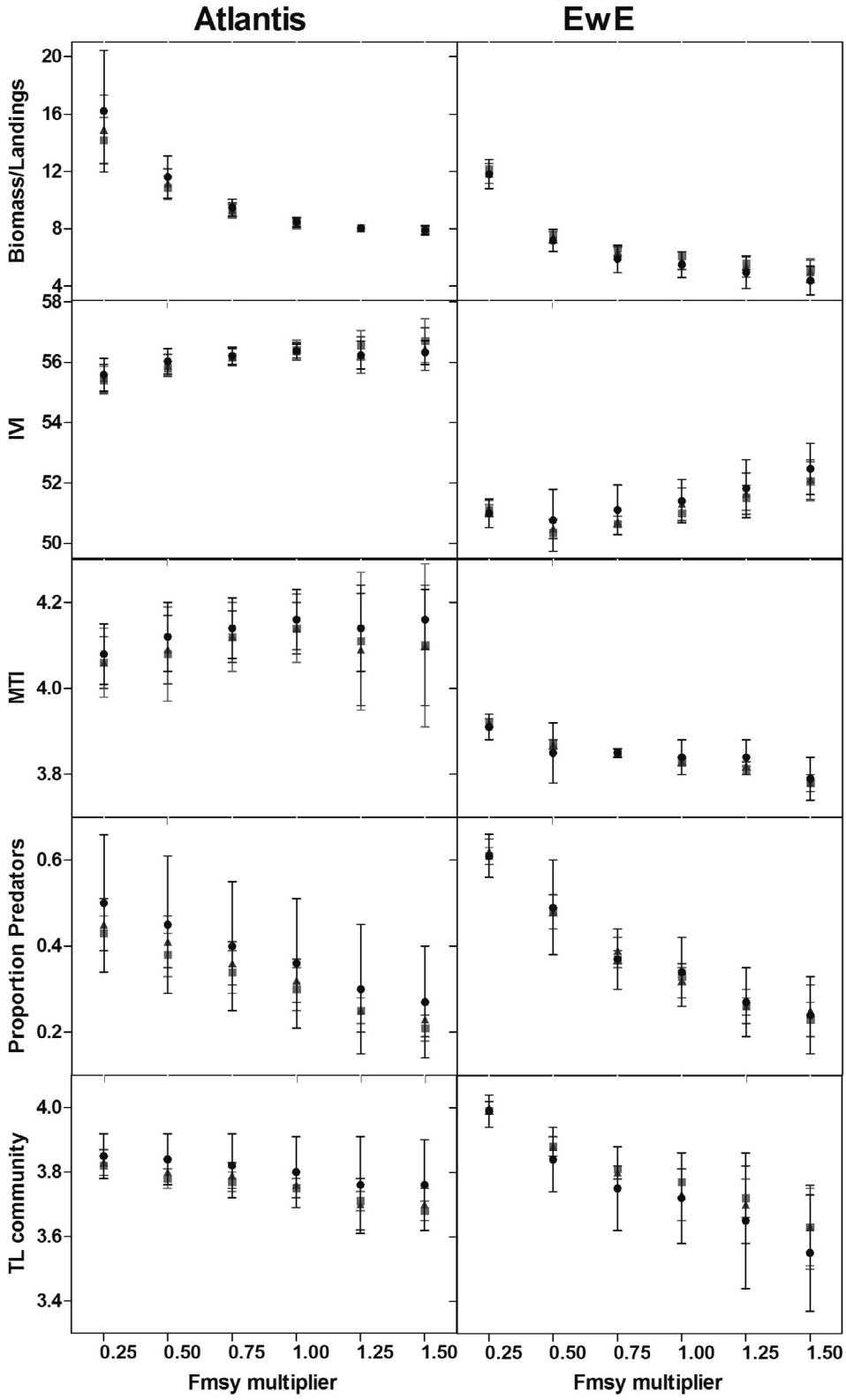

Fig. 6. Indicators (Mean ± SD) derived from the Atlantis and EwE models of the southern Benguela system for the HTL fishing strategy across F_{MSY} and random multipliers of phytoplankton biomass. Symbols represent the standard deviation values of the multipliers for the phytoplankton biomass, 0.1 = square, 0.2 = triangle and 0.3 = circle. IVI = Intrinsic vulnerability Index, MTI = Marine Trophic Index, TL community = Trophic level of the community.

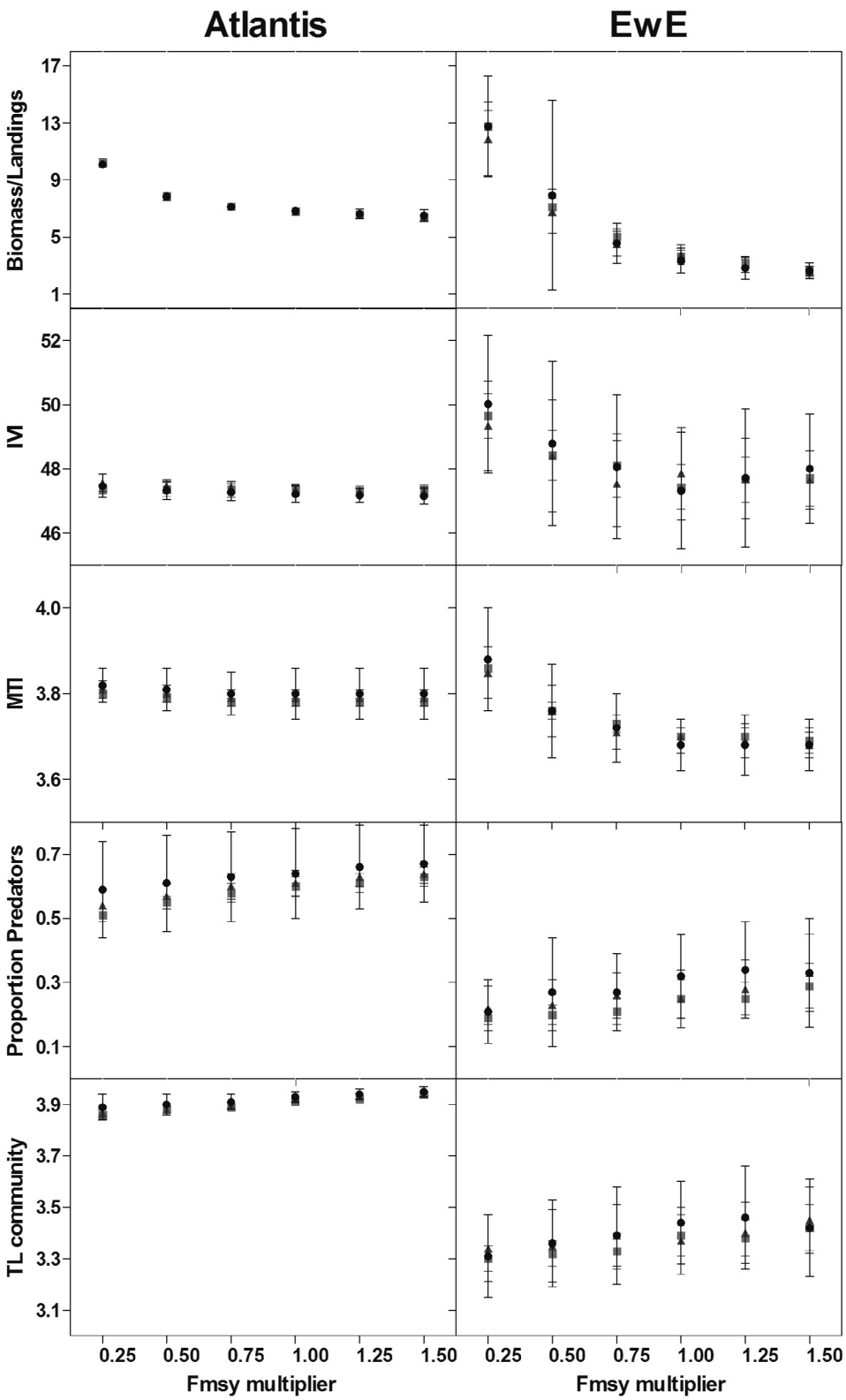

Fig. 7. Indicators (Mean ± SD) derived from the Atlantis and EwE models of the southern Benguela system for the LTL fishing strategy across F_{MSY} and random multipliers of phytoplankton biomass. Symbols represent the standard deviation values of the multipliers for the phytoplankton biomass, 0.1 = square, 0.2 = triangle and 0.3 = circle. IVI = Intrinsic vulnerability Index, MTI = Marine Trophic Index, TL community = Trophic level of the community.

3. Results

3.1. Comparison of indicators in output of Atlantis and EwE models of the southern Benguela

No systematic agreement was found in the indicator values derived from both models among fishing strategies and type of environmental change, especially for indicators such as IVI and MTI (Figs. 2–7). In terms of directional change, the largest overlap in values was recorded for the total biomass over catch ratio for the ALL fishing strategy (Fig. 2). Indicators such as the proportion of predators and the TL of the community also showed overlap in values between models for the ALL and HTL fishing strategy (Figs. 2 and 3). Major differences in indicators values were recorded under the LTL strategy between models, for instance, the proportion of predators ranged from 0.48 to 0.68 in Atlantis and from 0.16 to 0.40 for EwE, while the TL of the community ranged from 3.84 to 3.93 for Atlantis and 3.22 to 3.55 for EwE (Fig. 4). Interestingly, the two catch-based indicators IVI and MTI had consistent values between models under the LTL strategy (IVI: 47.12–47.83 for Atlantis and 46.5–50.68 for EwE), whereas under the ALL and HTL fishing strategies, the values differed between models by ± 2–4 for IVI and ± 0.07–0.28 for MTI.

Under random environmental change, the highest similarity in indicator values between models was recorded for the total biomass over catch ratio for all fishing strategies and less similarity for the IVI and MTI, with an overlap in values only recorded for the LTL strategy (Figs. 5–7). Despite the differences in indicator values between the two models, there was a good agreement in trends exhibited for most indicators and fishing strategies. All indicators computed from outputs of the EwE model showed a decreasing trend with increasing fishing pressure under the three fishing strategies, with the exception of the TL of the community and proportion of predators in the LTL strategy, and the IVI in the HTL strategy. These latter indicators are expected to increase with increasing fishing effort given the fishing strategies in play in each case. The increasing trend in IVI values in the HTL is explained by the increase in catches of HTL targets with increasing fishing pressure. Similarly, an increase in catches of LTL targets will cause a reduction in their biomass, explaining the increase in the proportion of predators and TL of the community in the LTL strategy. Indicators derived from the Atlantis model followed the expected trends, with the exception of IVI in the ALL strategy and MTI in the ALL and HTL strategies for both directional and random environmental change; in these cases these indicators increased with increasing fishing pressure. The increasing trend in MTI and IVI values was however subtle and differences in indicator values between the lowest and highest F_{MSY} multipliers were lower than 2 and 0.2 for IVI and MTI respectively.

Under the ALL and LTL scenario, the spread of indicator values across the range of directional change levels was notably larger for EwE simulations than for Atlantis simulations, whereas the spread in indicator values was similar in the HTL scenario. Specifically, indicators such as IVI and MTI derived from the Atlantis model showed a small spread among fishing multipliers and were not very responsive. Moreover, the TL of the community in the ALL fishing strategy showed small variability in values under both types of environmental change for the Atlantis model. Indicators such as IVI, MTI and the TL of the community were more responsive in the EwE model than in Atlantis model under the LTL scenario.

3.2. Indicator specificity under directional and random change

In terms of directional environmental change, the ratio of the mean fishing component of the gradient to the mean phytoplankton component of the gradient indicated that the total biomass over catch ratio had the highest specificity to fishing among fishing strategies for both ecosystem models (Fig. 8). The proportion of predators had the second highest specificity in the ALL and LTL strategies for the Atlantis model, while the MTI was the second most specific indicator in the EwE model. The majority of indicators influenced by directional change in the phytoplankton biomass were more specific to fishing (ratios > 1) in both models. For EwE, three out of five indicators under the LTL fishing strategy had low specificity (ratios < 1). For the Atlantis model, the IVI in the LTL and the TL of the community in the ALL fishing strategies showed low specificity, while the MTI of the ALL and LTL strategies and the TL of the community for the HTL strategy had specificity values close to 1. Although the specificity of most indicators was > 1, some indicators showed considerable variability (evidenced by their CI) such as IVI for both models, and the total biomass over catch ratio under the ALL and HTL strategies for EwE and Atlantis, respectively.

For the random environmental change, the total biomass over catch ratio was the most specific indicator to fishing in both ecosystem models as determined by the absolute slope of the signal-to-noise ratio with fishing mortality taken as the signal and the variable phytoplankton biomass as the noise (Fig. 9). The MTI was also among the most specific indicators for the EwE model, other indicators such as the TL of the community and the proportion of predators showed high specificity with random variability in the ALL and HTL scenarios. The proportion of predators was among the most specific indicators for Atlantis, high specificity was also recorded for the TL of the community in the LTL scenario and to a less extent in the HTL. The highest specificity for a given indicator was mostly recorded under the same fishing strategy in both models but not for the TL of the community and MTI. The specificity of ecosystem indicators usually decreased with increasing random variability (higher σ) in all scenarios based on EwE outputs. Using Atlantis, this general expectation was not true for the biomass over catch ratio in the HTL scenario, the IVI in the HTL and LTL scenarios, and the MTI in the HTL scenario (Fig. 9). Large confidence intervals were recorded for the total biomass over catch ratio in all strategies for both models, and IVI under all strategies in the EwE model.

4. Discussion

Studies of the sensitivity, responsiveness and specificity of indicators are necessary to evaluate indicator performance and their reliability when used to help achieve an effective ecosystem based management, since indicators of the effects of fishing must be able to respond primarily to fishing in the presence of environmental variability (Coll et al., 2016; Shin et al., 2010b). Our study evaluated the specificity of the response of selected ecosystem indicators to fishing in the southern Benguela system using two ecosystem models with different underlying assumptions and structures. A moderate to high specificity of indicators to fishing was demonstrated for the southern Benguela (specificity varied with the indicator, fishing strategy and type of environmental change), despite the importance of climate as a major driver of this upwelling system (Jarre et al., 2015; Shannon et al., 2004). Similarities in indicator and specificity values were recorded between models for indicators such as the total biomass over catch ratio, proportion of predatory fish and TL of the community under certain fishing strategies, reflecting the capacity of an indicator to capture ecosystem effects of fishing in the presence of environmental variability. The largest overlap between indicators values calculated from both ecosystem models was observed for the total biomass over catch ratio under both the directional and random environmental change scenarios. Both models (Atlantis and EwE) are sensitive to changes in phytoplankton biomass and by inference climate variability mediated through phytoplankton (and planktivorous groups) into the foodweb. Bottom-up control of small pelagic fish by zooplankton groups has been reported for upwelling systems in general (Cury et al., 2000; Shannon et al., 2014) and for the Southern Benguela in particular (Shannon et al., 2008, 2004).

Across both models most of the indicators followed the expected direction of change (i.e. decreasing with increasing fishing pressure),

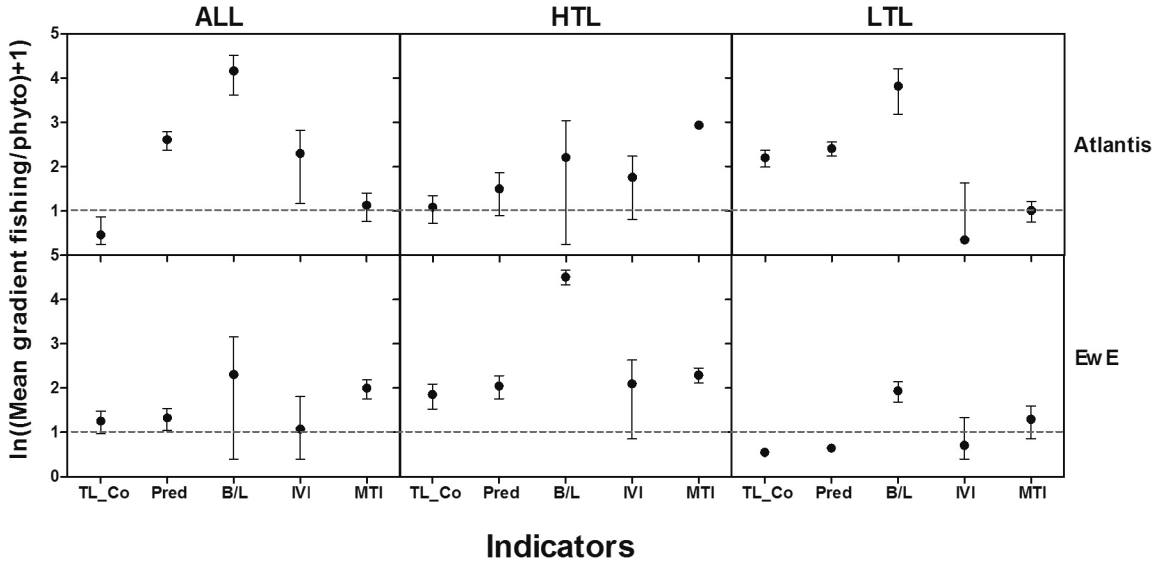

Fig. 8. Specificity (Mean ± 95% CI) of ecosystem indicators to fishing in the presence of directional environmental change across fishing strategies for both ecosystem models. ALL = All trophic levels strategy, HTL = high trophic level strategy and LTL = low trophic level strategy. TL_Co = Trophic level of the community, Pred = Proportion of predators, B/L = total biomass over catch ratio, IVI = Intrinsic Vulnerability Index and MTI = Marine Trophic Index.

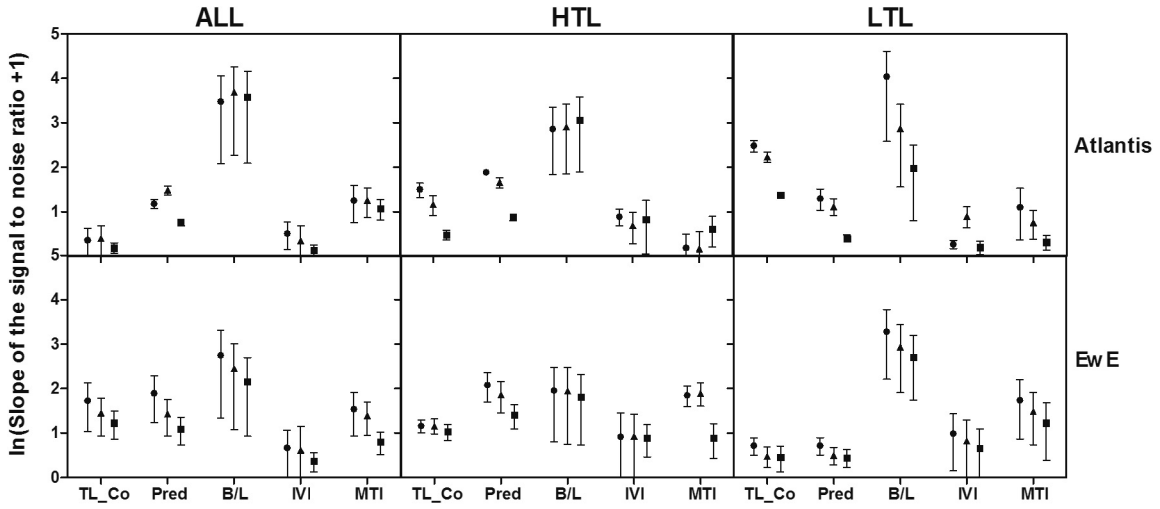

Fig. 9. Specificity (Mean ± 95% CI) of ecosystem indicators to fishing in the presence of random environmental change among fishing strategies for both ecosystem models. Symbols represent the σ multiplier, 0.1 = circle, 0.2 = triangle and 0.3 = square. ALL = All trophic levels strategy, HTL = high trophic level strategy and LTL = low trophic level strategy. TL_Co= Trophic level of the community, Pred = Proportion of predators, B/L = total biomass over catch ratio, IVI = Intrinsic Vulnerability Index and MTI = Marine Trophic Index.

with the indicators derived from both models yielding similar simulated responses to the effects of fishing. The most significant exceptions to these patterns were IVI and MTI in Atlantis, which did not consistently show the level of response and information content conveyed by the same indicator in the EwE model. The performance of the TL of the community in Atlantis was also poorer in comparison to the discernible response patterns seen for the EwE model. These differences are at least partly attributable to differences in the species/groups included as fisheries targets in each model. Mesopelagics, a low trophic level group (TL = 3.6 for our calculations) with high biomass, and chub mackerel are only fished in the EwE model not in Atlantis. The influence of these high biomass groups on the response of a catch-based indicator, such as MTI, means that their omission biases the Atlantis model result towards a response dominated by the behaviour of HTL targets. Similarly, the response of IVI (another catch-based indicator) in the Atlantis model was dominated by the response of HTL groups. IVI showed an increasing response to fishing pressure under the ALL strategy in Atlantis as was expected and observed under the HTL strategy, confirming this assumption. These results reinforce the findings of previous studies that noted the importance of species with a high biomass or dominant role in terms of their influence on ecosystem responses and the information content of indicators (Essington and Plagányi, 2014; Shin et al., 2018; Smith et al., 2011). Future studies exploring the sensitivity and/or specificity of indicators should include all species modelled in a system independently of whether they are surveyed or retained.

The agreement in the response of some indicators to increasing fishing pressure and environmental change between models strengthens confidence in the outcomes of these models. It also constitutes a first step towards bounding a range of plausible indicator values under different fishing and environmental variability scenarios for the southern Benguela. Further, our results highlighted that there are some important differences between indicators (e.g. IVI and MTI) calculated from the two model outputs that are likely attributed to differences in model structure and assumptions, and warrant further exploration. The agreement in performance of some indicators and patterns of change across models are in line with previous model comparisons for the

Southern Benguela, which reported similar responses (of the models and the set of indicators calculated based on their outputs) to fishing pressure between models of different types (Smith et al., 2015; Travers et al., 2010). System-level indicators such as the TL of the catch were reported to show more consistent trends than species-level biomass indicators in a comparison of Atlantis, EwE and OSMOSE models for the southern Benguela. However, system responses were dependent on the fishing strategy in place with ambiguous responses observed under a low trophic level strategy (Smith et al., 2015).

This study is one of a slowly accumulating set of multi-model comparison studies that evaluate the performance of indicators across ecosystem types. Here both models identified the total biomass over catch ratio as the most specific indicator to fishing under both types of environmental change (directional and random); this concurs with the finding of a broader evaluation of specificity of indicators which used ecosystem models of different types from seven marine ecosystems (from across the globe) (Shin et al., 2018). Total biomass, total landings and the proportion of exploited biomass were also identified as the most informative indicators of the dynamics of eleven ecosystems, also from across the world (Link et al., 2010). Houle et al., (2012) evaluated the sensitivity and specificity of ten ecosystem indicators using a theoretical, size-structured model, and found that the community biomass, mean TL of the community and catch to be among the least specific indicators. The evaluation of the TL of the community undertaken here and in previous model-based studies of the Benguela (Smith et al., 2015; Travers et al., 2010) would agree with this finding; while the indicator followed expected trends among models and showed high specificity under some fishing strategies, the magnitude of change in this indicator was minimal and so lacked sufficient contrast to allow meaningful interpretation in a management context. Smith et al. (2015) found the TL of the community to be more responsive to changes in fishing pressure in Atlantis compared to the EwE model, while we found the opposite. This discrepancy is because Smith et al. (2015) computed indicators using the biomass of twelve species common to the three models employed in that study, while the present study instead used all surveyed and retained species (pelagic- and benthic-feeding demersal fish and sharks were included in our study but not in Smith et al (2015), while they included mesopelagic fish in their study). Moreover, this study, calculated the TL of the community using fixed TLs for all model groups, meaning its capacity to detect the effects of fishing pressure is expected to be lower than if using variable species TL (Reed et al., 2016). Our results also indicate that the performance (specificity) of the TL of the community is influenced by the interaction of fishing and environmental scenarios. This is in agreement with previous work suggesting that the behaviour of an indicator depends on ecosystem traits (Heymans et al., 2014), fishing history and the pattern of fishing in an ecosystem (Shannon et al., 2014).

Previous studies have suggested that indicators should be tested for a particular ecosystem before they are used to support management decisions to understand their responses and variability (Fulton et al., 2005; Houle et al., 2012). Our study has shown that while both catch- and community-based indicators can be specific to fishing pressure under environmental variability, the total biomass over catch ratio reacts most strongly to fishing across all fishing strategies considered, whereas others indicators seem better suited to tracking the effects of fishing under one or other fishing strategy (e.g. TL of the community appears most useful in an HTL fishing strategy). In line with previous studies (Fulton et al., 2005; Large et al., 2013; Link, 2005; Shin and Shannon, 2010), our results underline the need to use indicators as an ensemble rather than relying solely on a single indicator, since they provide information on different aspects of ecosystem status. Similarly, our results highlighted that it is important to consider the response of a given indicator based on the fishing strategy in place on an ecosystem. Further, given that higher specificity of ecosystem indicators to fishing was generally recorded at lower levels of variability of phytoplankton biomass in this two-model case study, and recognising the expected increase in environmental variability and directional change associated with climate change (Henson et al., 2017; Ummenhofer and Meehl, 2017), this study provides an important first step in evaluating the robustness of indicators to fishing in the presence of environmental change for the southern Benguela.

Model results presented in this study are encouraging in that i) general patterns of specificity of indicators to fishing under environmental change seen across a variety of marine ecosystems were shown to hold for the Southern Benguela Upwelling Ecosystem; ii) the results of the current study are consistent (robust) in terms of the response of most indicators across two modelling approaches with fundamentally different underlying assumptions; and iii) certain indicators are better suited to tracking fishing effects under certain fishing scenarios, supporting the use of an ensemble of ecological indicators in an EAF. Future studies should extend this work by using other environmental drivers predicted to experience strong (or highly uncertain) future changes as the main forcing of simulation experiments to improve realism and confidence in the evaluation of ecosystem indicators, as future changes in environmental drivers may influence the specificity of indicators or interact in unexpected ways with one another and/or with fishing as a driver.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolind.2018.07.021.

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